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A methodology for parameter estimation in seaweed productivity modelling

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Abstract

This paper presents a combined approach for parameter estimation in models of primary production. The focus is on gross primary production and nutrient assimilation by seaweeds.

A database of productivity determinations, biomass and mortality measurements and nutrient uptake rates obtained over one year for *Gelidium sesquipedale* in the Atlantic Ocean off Portugal has been used. Annual productivity was estimated by harvesting methods, and empirical relationships using mortality/wave energy and respiration rates have been derived to correct for losses and to convert the estimates to gross production.

In situ determinations of productivity have been combined with data on the light climate (radiation periods, intensity, mean turbidity) to give daily and annual productivity estimates. The theoretical nutrient uptake calculated using a 'Redfield ratio' approach and determinations of *in situ* N and P consumption by the algae during incubation periods have also been compared.

The results of the biomass difference and incubation approaches are discussed in order to assess the utility of coefficients determined *in situ* for parameter estimation in seaweed production models.

Introduction

Incubation techniques have provided a good deal of information on the photosynthetic and respiratory rates of different species (e.g. Brinkhuis, 1977; Búesa, 1977; Arnold & Murray, 1980; Torres *et al.*, 1991). On the other hand, many estimates of annual productivity of macrophyte algae have been carried out by means of harvesting methods (e.g. Mann, 1973, Murthy *et al.*, 1986).

Short-term incubation of algae for photosynthetic and respiratory determinations have to be employed carefully because of possible alterations in apparent photosynthetic rates due to nutrient limitation (Búesa, 1977), oxygen tension (Dromgoole, 1978a), carbon depletion or pH change (Dromgoole, 1978b), age structure, morphological and physiological state (Littler & Arnold, 1980). Besides that, photosynthetic studies may free the plant from constraints such as crowding and self-shading effects so producing overestimates of *in situ* photosynthetic rates. The results obtained with incubation techniques can be extrapolated to the population level only if biomass standing stocks are assessed and if the photosynthetic response of the algae to different physical and chemical factors is known. Biotic interactions such as competition and predation must also be considered.

Harvesting techniques are beset with a number of problems, namely the usually high variability of biomass standing stocks and the difficulties to quantify precisely the dead and decaying parts, as these fractions often do not accumulate *in situ* (Murthy *et al.*, 1986). One of the possible ways to quantify mortality losses is through tagging of algal fronds.

The objective of this work was to combine productivity and respiratory rates determined by incubation methods with harvesting and tagging techniques for parameter estimation in the development of a productivity/biomass model. The agarophyte *Gelidium sesquipedale* was chosen for this study because of its economic importance as the principal raw material for the Portuguese agar industry (Santos & Duarte, 1991).

Materials and methods

Study area

Sampling was carried out at a depth of 9–13 m at a *G. sesquipedale* harvest area off the west coast of Portugal, over a 17 month period with the help of scuba divers.

Macrophyte biomass

Five 0.16 m^2 quadrats were collected monthly. The number and size of the quadrates were determined by Santos (*in verbis*) so as to minimize sampling errors and time of sampling. The algae were washed to remove epifauna and epiphytic species, dried to constant weight at 75 °C, allowed to cool and their biomass determined.

Incubation experiments

Samples for the determination of production rates by the light-dark bottle technique were collected monthly. Immediately after collection the algae were incubated in 1000 ml jars at 9 m depth for 1 hour. Incubation times and biomasses were chosen so as to prevent inhibition of photosynthesis by an excess of dissolved oxygen or by nutrient depletion and simultaneously assuring detectable oxygen changes (Dromgoole, 1978a; Duarte, unpublished).

Several whole plants were incubated in each bottle in order to simulate the self-shading effects occurring in natural conditions. Six replicates (light and dark) were incubated with algae, and two controls were used to assess the effect of planktonic primary production and respiration.

After the incubation period, water samples for dissolved oxygen determination by the Winkler method and for nutrient analysis were collected. The algae used in each experiment were blotted dry and dried at 75 °C to constant weight, allowed to cool and weighed. The conversion of oxygen values to mg carbon fixed g^{-1} dry weight h^{-1} was carried out assuming a P.Q. of 1.2 (Vollenweider, 1974).

Tagging experiments

Over a yearly period 100–200 tagged algae were monitored in order to assess the mortality of the population by the decline of tagged plants and to compare the elongation rates of plants with and without epiphytic algae.

Physical and chemical parameters

During the field incubation experiments water temperature, Secchi disc readings and nutrient samples were taken. The light at the sea surface was determined from hourly total radiation data obtained for the period of study. The corresponding photon flux density below the sea surface (PFD) was computed according to the Lambert-Beer law considering that

1. the photosynthetically active radiation corresponds to 42% of the overall incident radiation (Margalef, 1977);
2. the losses related to the angle of incidence of the sunlight and the wind stresses on the sea surface decrease further the incident radiation by an average of 15% (Parsons, *et al.*, 1984);
3. the light path between the surface and the desired depth depends on the depth and the incidence and refraction angles of the sun light (Rable; 1985);
4. extinction coefficients were determined empirically from the Secchi disc readings.

Conceptual basis for modelling

Forcing functions

The model uses surface light intensity, water temperature and wave power as forcing functions to simulate the productivity, respiration and biomass variations of the algae.

Model structure

The model is separated in three sub-models:

(i) Sub-model for tidal height simulation;
Calculates the depth of the simulated algal population at every time step as described by Ferreira & Ramos (1989).

(ii) Sub-model for submarine light intensity simulation;
This sub-model uses global radiation data obtained at sea surface level, time and depth as inputs, to calculate the corresponding light intensity below the sea surface as stated above. An average extinction coefficient of 0.264 was used for the model simulations, based on Secchi disc readings.

(iii) Productivity/biomass sub-model;
The sub-model equations are presented in Table 1. Biomass variations are calculated as shown in equation (1). This sub-model uses empirical relationships between productivity versus PFD and temperature values and between respiration and temperature, obtained from the incubation experiments (equations 2, 3 and 4 from Table 1).

Results and discussion

Chemical factors, such as nutrient concentrations in sea water and biotic factors, such as grazing and competition were not considered in the model. Nutrient limitation is difficult to assess because of the capacity of *Gelidium* species, as well as other algae for luxury consumption and accumulation of nutrients during periods of high availability which can then be used in periods of low availability (Fredriksen & Rueness, 1989; Fujita *et al.*, 1989).

During all the field work there was no clear evidence of grazing of *G. sesquipedale* by fish or invertebrate species. Concerning competition with epiphytes, although species like *Ploccamium coccineum*, *Asparagopsis armata* or *Dyctiota dichotoma* could be potential competitors of *G. sesquipedale* for light and nutrients, especially in summer when those species become particularly abundant (Duarte, *in prep.*), the average growth rates of tagged *G. sesquipedale* fronds with and without epiphytic algae were not significantly different (t-test $p<0.05$). Our results are in good agreement with the findings of Melo *et al.* (1991) for *G. robustum* and *G. nudifrons*. According to these authors there is no evidence that growth rates of those *Gelidium* species are affected by animal or plant epiphytic loads.

Table 1. Model equations

$$\frac{\mathrm{d}b}{\mathrm{d}t} = (\mathrm{PROD}_t - \mathrm{RESP}_t - \mathrm{EXSUD}_t - \mathrm{MORT}_t)\, b\, \mathrm{Y} \ (1)$$

$$\mathrm{PROD}_t = \frac{1}{z_1 - z_0} \int_{z_0}^{z_1} \mathrm{PROD}_z \,\mathrm{d}z \ (2)$$

$\mathrm{PROD}_z = f$ (light intensity, temperature) (3)
$\mathrm{RESP}_t = f$ (temperature) (4)
$\mathrm{EXUD}_t = f(\mathrm{PROD}_t)$ (5)
$\mathrm{MORT}_t = f$ (wave power_t) (6)

b – biomass (g m^{-2}), t – time (h), Y – conversion factor of mgC to g dry weight, PROD_z – productivity ($\mathrm{mgCg}^{-1}\,\mathrm{h}^{-1}$) at depth z (m), PROD_t – depth integrated productivity ($\mathrm{mgCg}^{-1}\mathrm{h}^{-1}$) at time step t, z_0 and z_1 – minimal and maximal depths (m) for productivity calculation, RESP_t – respiration ($\mathrm{mgCg}^{-1}\mathrm{h}^{-1}$) at time t, EXUD_t – exudation rate ($\mathrm{mgCg}^{-1}\mathrm{h}^{-1}$) at time t, MORT_t – mortality ($\mathrm{mgCg}^{-1}\mathrm{h}^{-1}$) at time t.

Parameter estimation

Figure 1 shows the productivity rates as measured by means of incubation experiments and corresponding PFD. A two-order polynomial gives a good fit between PFD and productivity.

Temperature and productivity are positively correlated ($p < 0.05$). This result is confirmed by the findings of Macler & West (1987) in Macler & Zupan (1991) and Torres *et al.* (1991) for other *Gelidium* species.

The combination of the polynomial shown in Fig. 1 with a nondimensional temperature limiting factor significantly improves the fit to the obtained data ($r = 0.712$, $p < 0.005$, average error = 17%) (Fig. 2):

$$\mathrm{PROD}_z = (0.538 + 0.007\,\mathrm{PFD} - 1.6 \times 10^{-5}\,\mathrm{PFD}^2)\left(\frac{\mathrm{Temperature}}{\mathrm{Tlim}}\right)^{\beta},$$

where,

PFD = Photon flux density (μmol m^{-2} s^{-1});
Tlim = Limiting temperature;
β = dimensionless constant.

Tlim and β were determined by a least squares interactive procedure. The values obtained were respectively 17.2 and 0.5.

For light intensity values below the minimum PFD (PFD′) used for the polynomial fit, PRODz was calculated according to the expression

$$\mathrm{PROD}_z = \left(\mathrm{PROD}_z' \frac{\mathrm{PFD}}{\mathrm{PFD}'}\right)\left(\frac{\mathrm{Temperature}}{\mathrm{Tlim}}\right)^{\beta},$$

where, PRODz′ = observed productivity under PFD′. PRODz values for each time step are integrated over depth according to the equation (2) of Table 1.

The shape of the curve shown in Fig. 1 is that of a photosynthesis versus irradiance curve with photoinhibition. In fact, the lowering of productivity at PFDs above 200 μmol m^{-2} s^{-1} cannot be explained by low temperatures or nutrient contents as those points correspond to spring and early autumn measurements.

Figure 3 shows the positive relationship between respiration and temperature. The regression obtained was used in equation (4) of Table 1 to calculate respiratory rates.

Mortality rates estimated from the losses of tagged plants were correlated to wave power values obtained by the model MAR 211 (Pires & Rodrigues, 1988). A regression equation was used to compute the former from the latter (Fig. 4).

Exudation rates are computed as a proportion of gross primary productivity (GPP) according to Khailov & Burlakova (1969). Model parameter optimization led to the adoption of a value of 20%.

At each time step the 'new' biomass is computed from the 'old' biomass plus the result of equation (1). GPP is calculated as the sum of all biomass produced. Net Primary Productivity (NPP) is computed as GPP minus respiration and exudation as calculated by the model.

Model simulations

The model was used to simulate the biomass variation and to estimate the daily and annual productivity of *G. sesquipedale*. Two different approaches were used:

(1) The observed biomass at the beginning of the sample work (May 1990) was used as the starting value for the model;
(2) The biomass values measured during the period covered by the simulation (Fig. 1) were used as inputs to the model at the corresponding dates.

These two approaches allowed an evaluation of the model performance both in the short and long term.

In order to assess the accuracy of the model in

Fig. 1–6. Fig. 1. Gross Productivity (GPP) ± 95% confidence limits as a function of Photon Flux Density (PFD). *Fig. 2.* Measured (± 95% confidence limits) and simulated Gross Productivity (see text for explanation). *Fig. 3.* Respiration (R) ± 95% confidence limits as a function of temperature. *Fig. 4.* Daily mortality, calculated as the decline rate of tagged fronds per day, as a function of average daily wave power. *Fig. 5.* Biomass density ± 95% confidence limits between May 1990 and

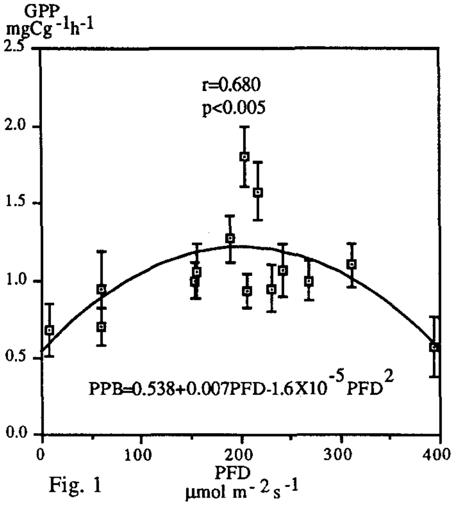

Fig. 1

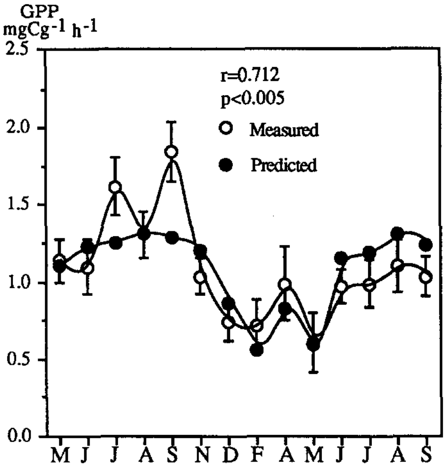

Fig.2

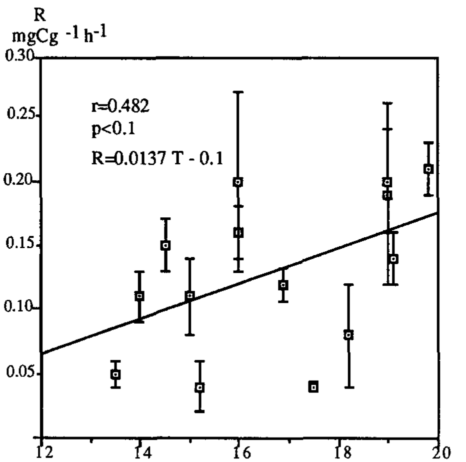

Fig. 3

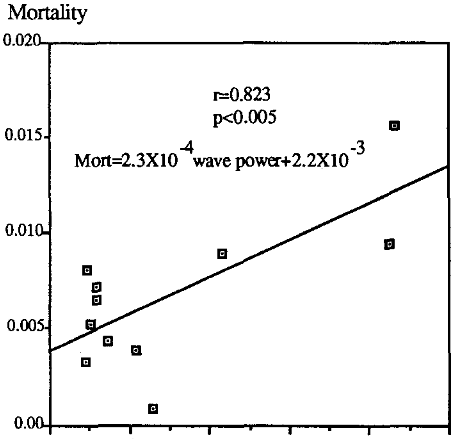

Fig. 4

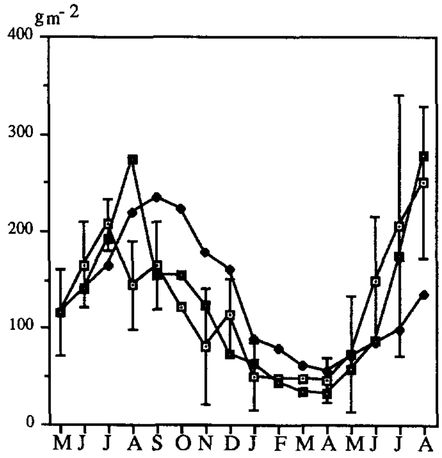

Fig. 5

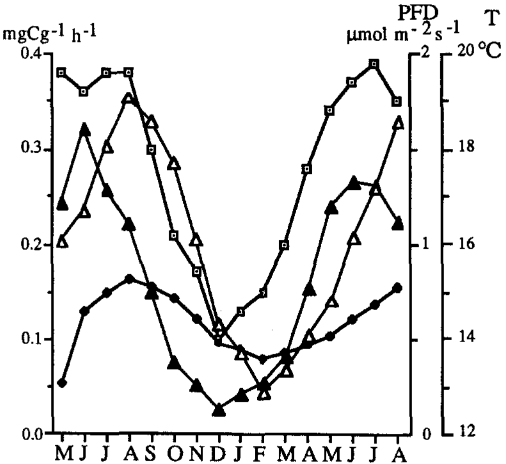

Fig. 6

August 1991 calculated by sampling —□— (values without error bars were interpolated), by model simulation 1 —◆— and model simulation 2 —□— (see text for explanation). *Fig. 6.* Simulated average hourly Gross Productivity —□— and respiration —◆— (left axis) and, Photon Flux Density —▲— (right axis) from May 1990 to August 1991. Average monthly temperature is shown for the same period —△—.

the estimation of NPP the method of Wiegert & Evans (1964), as adapted by Murthy *et al.* (1986) was used. Another approach for NPP evaluation was based on the sum of biomass differences with mortality (computed from the loss rates of tagged plants). The results obtained by these two methods and by the two model simulations are summarized in Table 2.

Method 1 will probably tend to overestimate productivity as it assumes that a fall between two successive biomass peaks corresponds to biomass which was produced and removed during the corresponding period. Method 2 is probably more accurate because it uses estimates of biomass removal based on the loss rate of tagged plants and assuming that the observed rate is equal to the rate of biomass loss.

The differences between the two model simulations are negligible and the differences between simulation 1 and the results obtained by Methods 1 and 2 are respectively of 31 and 20%. The model estimates NPP quite accurately even over a yearly period. The GPP annual values are also shown in Table 2. Biomass losses by respiration and exudation calculated by the model simulation 1 are used to compute the GPP values obtained from method 1 and 2.

Figure 5 represents the biomass density variation between May 1990 and August 1991. Maximal values were reached in summer, always below 300 gm^{-2} dry weight (dw). Minimal values were observed during winter and early spring when the biomass reached values as low as 50 gm^{-2} dw. The predicted values by both model simulations are also shown in Fig. 5. The model provides a reasonable representation of biomass density variation In model simulation 2 explicit computation of mortality and exudation led to biomass predictions closer to the observed values than those obtained by previous authors (Brinkhuis, 1977; Ferreira & Ramos, 1989).

Table 2. Net and gross primary productivity estimated from the model and calculated by two biomass difference methods (see text). All results in g m^{-2} yr^{-1}

	NPP	GPP	References
Method 1	382	953	Wiegert & Evans (1964), Murthy *et al.* (1986)
Method 2	329	900	This work
Simulation 1	263	834	This work
Simulation 2	259	761	This work

It can be seen from Fig. 6 that the peaks of PFD and temperature occur in spring and in summer respectively. The peaks in productivity predicted by the model occur in summer, showing that the fall in PFD is compensated by temperature.

The model can be used to estimate the nutritional needs of *G. sesquipedale*, and this is of major importance when cultivation is considered. Assuming a carbon content of 32.5% (dw), a nitrogen content of 3.5% (dw) Torres *et al.* (1991), and a phosphorus content of 0.074% (dw) (Duarte, *in prep*) the average (daily C, N and P fixation calculated from the GPP result of model simulation 1 is respectively 271.00, 29.01 and 0.32 gm^{-2}.The knowledge of the average biomass density allows the calculation of the average hourly N and P removal per g of dw. Computed over a year the result is 1.5 μmol N g^{-1} h^{-1} and 0.016 μmol P g^{-1} h^{-1}. The consumption of nutrients in the incubation vessels gave highly variable results among replicates. Most of the times it was not possible to detect any significant variation. However, a rough estimate of ammonium plus nitrate nitrogen consumption gives results which can reach 5 μM N g(dw)$^{-1}$ h^{-1} whilst the uptake of phosphate is not higher than 0.64 μM P g(dw)^{1} h^{-1}. Thus it can be concluded that the model estimates are well within the limits of the nutrient uptake rates measured during the incubation experiments.

The sensitivity of the model to the extinction coefficient (k) was tested. A 10% decrease on the averaged k of 0.264 produces a NPP increase by two orders of magnitude, a 10% decrease has an opposite effect of the same magnitude.Thus the choice of k is obviously critical.

Once the relation between dry weight and length is known

$$\text{weight} = -8.631 \times 10^{-3} + 3.773 \times 10^{-3}\,\text{length} + 3.799 \times 10^{-4}\,\text{length}^2$$

(for plants of more than 2 cm).

the model (equations 2, 3, 4 and 5) can be used to simulate the growth rates of individual fronds. This allows the computation of the time a plant will take to reach an harvestable size. By simulation it was possible to conclude that if the population is cut to an average size of less than 3 cm in length it will not reach an harvestable size until the next harvest season (assuming 12 cm as the minimum harvestable size).

The model was written and compiled in Quick Basic for IBM compatible and Macintosh computers. It can be employed with minor adaptations to different species of primary producers, namely in the domain of resource management and ecological modelling.

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